

THE POTENTIAL OF THE INVASIVE SNAIL *POMACEA CANALICULATA* AS A PREDATOR OF VARIOUS LIFE-STAGES OF FIVE SPECIES OF FRESHWATER SNAILS

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ABSTRACT

The invasive apple snail *Pomacea canaliculata* is known as an omnivorous species, but there are only few reports of its predation. This study examined the potential of this snail as a predator of common freshwater snails in southern China. Laboratory experiments were conducted to quantify the damage of the apple snail to both early stages (eggs and/or neonates) and adults of five species of freshwater snails (*Austropeplea ollula*, *Biomphalaria straminea*, *Melanooides tuberculata*, *Physa acuta*, *Sinotaia quadrata*). The apple snail caused significant mortality to all of the early stages of the five snails, as well as adults of the pulmonates *A. ollula*, *B. straminea* and *P. acuta*, but did not consume adults of the prosobranchs *M. tuberculata* and *S. quadrata*. Such differential survival of the prey might be explained by differences in shell hardness and structure, as the adult prosobranchs were well protected by a hard shell and an operculum, whereas the pulmonates had a relatively fragile shell and lacked an operculum. The apple snail was unable to detect its prey from a distance, but it crawled quickly, which could create opportunities for direct contact with potential prey. Apple snails may therefore influence invaded ecosystems through predation on other freshwater snails.

Key words: apple snail, invasive species, crushing resistance, *Pomacea*, predation.

INTRODUCTION

The golden apple snails, *Pomacea canaliculata* (Lamarck, 1822) and *P. insularum* (d'Orbigny, 1835) (Mollusca: Ampullariidae), are native to the freshwater wetlands of South America, but have been widely introduced into Asia and into North and Central America since the 1980s as aquarium pets or human food (Cowie, 2002; Estebenet & Martín, 2002; Joshi & Sebastian, 2006; Rawlings et al., 2007; Hayes et al., 2008). These species possess several traits of successful invasive species. Under favorable conditions, they can reach a life-span of up to four years (Estebenet & Cazzaniga, 1992), attain maturity in 2 to 4 months (Estoy et al., 2002), and each female can lay up to 8,680 eggs per breeding season (Miyahara et al., 1986). They are highly adaptable to harsh environmental conditions, such as low dissolved oxygen concentration, high nutrient content, low food supply, and low temperature (Cowie, 2002).

In its invaded regions, *Pomacea* spp. are mainly known as agricultural pests. They are

voracious feeders on wetland crops, causing tremendous loss to the rice paddies of Asia and taro farms of Hawaii (Naylor, 1996; Halwart, 1994; Cowie, 2002; Joshi & Sebastian, 2006). Apart from crops, these species have also been reported to feed on wild macrophytes. For example, Estebenet (1995) and Lach et al. (2000) conducted laboratory experiments to study the feeding of *P. canaliculata* on some common aquatic macrophytes in Argentina and Hawaii, respectively. They found that the snails exhibited a clear preference for certain macrophytes, and that their growth rates were high when fed with the preferred macrophytes. In the field, Carlsson et al. (2004) found high densities of *P. canaliculata* to be associated with low diversities of aquatic macrophytes, high nutrient concentrations, and high phytoplankton biomass in wetlands. Herbivory by apple snails caused a loss of wild macrophytes (Carlsson et al., 2004; Carlsson & Lacoursière, 2005), and a change towards dominance by phytoplankton (Carlsson et al., 2004).

Previous studies have thus highlighted the important herbivorous impact of *Pomacea*

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canaliculata on crop production, wetland floral diversity, and ecosystem functioning. However, relatively few studies have been conducted to determine the impact of these invasive gastropods on other aquatic invertebrates. Cazzaniga (1990) reported predation by *P. canaliculata* on eggs, neonates, and adults of the gastropod *Biomphalaria peregrina*. Cha (1989) reported predation of *P. canaliculata* on eggs and neonates of *Biomphalaria straminea* and on the neonates of three other snail species (*Austropeplea ollula*, *Physa acuta*, *Melanoides tuberculata*), but no predation on the neonates of another snail (*Sinotaia quadrata*). Wood et al. (2006) reported that *P. canaliculata* grazed actively and selectively on freshwater bryozoans. Nevertheless, these studies were conducted without offering food to the predator before the experiment (Cha, 1989) or during the experiment (Cazzaniga, 1990; Wood et al., 2006). It remains unknown whether non-starved *P. canaliculata* will prey on other invertebrates when alternative food is available, how the predator detects its prey and what determines the vulnerability of the prey.

This study examined the potential of *Pomacea canaliculata* as a predator of the early stages as well as adults of five species of snails commonly found in the freshwater wetlands of southern China. Each species of potential prey was kept with *P. canaliculata* for a certain period of time in laboratory aquaria, after which prey mortality was recorded. To understand whether shell hardness plays a role in the relative vulnerability of the potential prey, their crushing resistance was determined and a relationship between shell length and crushing resistance established for each species. To understand the mechanism underlying prey selection, tests were conducted to examine the crawling behaviour of *P. canaliculata* and determine whether it could detect prey from a distance.

METHODS

Potential Prey Species

The experiments were conducted between February 2007 and April 2008 at Hong Kong Baptist University (HKBU). Five species of snails were used: *Austropeplea ollula* (Gould, 1859) (Lymnaeidae), *Biomphalaria straminea* (Dunker, 1848) (Planorbidae), *Physa acuta* Draparnaud, 1805 (Physidae), *Melanoides tuberculata* (Müller, 1774) (Thiaridae), and *Sinotaia quadrata* (Benson, 1842) (Viviparidae).

These species are common in freshwater wetlands of southern China. The first three species are pulmonates, whereas the last two are prosobranchs. The three pulmonates are oviparous, laying submerged egg masses. The two prosobranchs are ovoviviparous, retaining eggs and developing embryos in the body, and giving birth to free-crawling juvenile snails. For the oviparous species, tests were performed on the egg masses, neonates, and adults. For the ovoviviparous species, tests were performed on the neonates, juveniles and adults of various sizes.

Collection and Maintenance of Test Animals

Juveniles and adults of the potential prey were collected from various shallow water environments (semi-aquatic vegetable farms, irrigation channels, and ponds) in the New Territories, Hong Kong. They were reared at Hong Kong Baptist University in separate stock aquaria containing 50 L dechlorinated tap water at $22 \pm 1^\circ\text{C}$. Aeration was provided to each aquarium with an air pump via plastic tubing and an air stone. Approximately 1/3 of the water was changed twice a week to avoid fouling. A commercial fish meal was fed *ad libitum* to the snails three times a week. Leaves of romaine lettuce (*Lactuca sativa* var. *longifolia*) were also supplied to the species that feed on plants (*A. ollula*, *B. straminea* and *P. acuta*). Under these conditions, the snails grew and reproduced successfully. Juveniles and adults of the potential predator, *P. canaliculata*, were collected from an irrigation channel in Yin Kong Village, the New Territories, and reared in an aquarium containing 80 L dechlorinated tap water and fed with romaine lettuce. All other rearing conditions for *P. canaliculata* were the same as those for the potential prey species.

Experiment 1. Predation of *P. canaliculata* on Eggs, Juveniles and Adults of the Potential Prey

For each prey species, tests of predation by the apple snail on a particular life stage were run using three aquaria, each containing 8 L dechlorinated tap water. Three aquaria with the prey but without *P. canaliculata* were used as experimental controls. Two size classes of apple snails (12–15 mm and 37–40 mm shell length) were tested separately. Since this apple snail becomes mature at around 25 mm shell length (Estebenet & Martín, 2002; Estoy et al., 2002), the smaller individuals were juveniles

and the larger individuals were adults. The experimental temperature was the same as that used in rearing the juveniles and adults. In addition to the following quantitative tests, direct observation of the predatory behavior of *P. canaliculata* was also conducted in separate aquaria.

In tests of predation on egg masses of the three pulmonate species, 20 to 40 adults of a prey species were transferred from the stock aquarium into each of the experimental aquaria and kept for up to three days. When each aquarium contained more than 25 egg masses, the adults were removed. The egg masses of these species are gelatinous, ranging from 3.5 to 5.5 mm in diameter, each containing 15 to 30 embryos. They were laid on the bottom and walls of the aquaria, and were visible with the naked eye. After marking the positions of these egg masses, an individual of *P. canaliculata* was introduced into each aquarium. To determine if there was an ontogenetic shift in predation, both juvenile and adult *P. canaliculata* were used in separate tests. Romaine lettuce was provided *ad libitum*, and the aquaria were covered with an opaque plastic bag to avoid directional effect of light on snail movement. To avoid the potential effect of laboratory predatory experience on predation rate, each individual of *P. canaliculata* was used only once. After 24 h, the aquaria were inspected and the numbers of egg masses remaining intact, that were damaged, and that had disappeared were recorded. Preliminary observation had shown that the egg masses would remain intact and attached to the bottom/walls of the aquaria until the juveniles hatched. Since it took at least five days for the embryos to develop into juveniles and hatch (Kwong, unpublished data), predation was considered to be the cause of disappearance of egg masses.

In tests of predation on neonates (i.e., individuals hatched within the previous 24 h), each aquarium contained 60 ± 5 neonates. The neonates of the three pulmonates were of similar sizes, with approximately 1 mm maximum dimension (shell width or shell height). The neonates of the two prosobranchs were similar in size (approximately 3 mm shell length) but much larger than those of the pulmonates. Three individuals of *P. canaliculata* were introduced into each test aquarium. After 72 h, the numbers of neonates alive, dead and that had disappeared were recorded, and the shells examined for signs of attack.

In tests of predation on adults, 15 individuals of a potential prey species were introduced into

each aquarium together with three individuals of *P. canaliculata*. The size range of the prey was 7–8 mm shell width (SW) for the disc-shaped *B. straminea*, and 13–15 mm shell length (SL) for *A. ollula*, 10–12 mm for *P. acuta*, 23–26 mm for *M. tuberculata* and 25–30 mm for *S. quadrata*, all of which are species with tall, narrow shells. Although different in size, they were all relatively large mature individuals of the respective species. Two whole leaves of romaine lettuce (fresh weight 30 ± 5 g) and 30 mg of fish meal (Hakari® Algal Wafer) were provided as food for the snails during the experiment. In 24 h, apple snails consumed less than half of food offered. Excessive food was removed, and new food was offered daily. After 72 h, the number of dead individuals in each aquarium was recorded and the shells examined for signs of attack.

Experiment 2. Size-dependent Predation of *P. canaliculata* on Two Prosobranchs

Experiment 1 showed that adult *P. canaliculata* preyed upon the neonates of *M. tuberculata* and *S. quadrata*, but not on the large adults of these prosobranchs (see Results). This follow-up experiment examined whether apple snails could prey on the juveniles and smaller adults of the two prosobranchs. In total, 111 *M. tuberculata* and 84 *S. quadrata* were used. These individuals ranged from neonates to large adults (3–28 mm SL). For each prey species, all individuals were introduced into an aquarium containing 25 L water and 10 adults of *P. canaliculata* (35–40 mm SL). Fish meal and romaine lettuce were fed to the snails *ad libitum*. Water was changed daily to avoid fouling. After 3 days, living prosobranchs were collected from each aquarium and their shell lengths measured. The shell length frequency data before and after the experiment were compared.

Experiment 3. Crushing Resistance of Different Prey Species

The crushing resistance of the five species of prey was determined using a mechanical crusher. This device consists of a heavy duty lab jack, an electronic balance (maximum weight: 10 kg, precision: ± 0.001 kg) for measuring the crushing strength, and a stainless steel vice for holding the specimens. The whole rig was mounted vertically and vertical movement was achieved by a rotary mechanism on the jack. During measurement, a live prey individual was

placed in the vice and the crushing weight read directly from the electronic balance. For the disc-shaped *B. straminea*, force was directed through the body whorl perpendicular to the periphery of the shell. For the other four species, force was directed along an axis perpendicular to the columella (Lewis & Magnuson, 1999). The vice was tightened by the jack until the shell was crushed. During this process, the force was gradually increased up to the sudden event of shell collapse. The maximum reading was taken as the crushing resistance. For each species, the measurements covered a size range from young juveniles to large adults (3.0–17.5 mm SL for *A. ollula*, $n = 69$; 2.0–5.7 mm SW for *B. straminea*, $n = 49$; 2.4–10.0 mm SL for *P. acuta*, $n = 63$; 3.2–19.0 mm SL for *S. quadrata*, $n = 83$; and 3.0–28.0 mm SL for *M. tuberculata*, $n = 77$). However, the smallest pulmonates (≤ 2 mm SL or SW) were too fragile to be measured using this method. The data were used to establish a relationship between shell width/length and crushing resistance for each prey species.

Experiment 4. Prey Detection and Crawling in *P. canaliculata*

Assays of prey detection by *P. canaliculata* were performed using a circular plastic basin (diameter 60 cm, depth 10 cm). With six equally spaced acrylic plates extending 20 cm from the wall to the center, the basin was partitioned into six fan-shaped side compartments and a central circular compartment. Three alternate side compartments were randomly assigned as replicates, each containing the prey species. A fixed number of adults of one prey species (15 individuals of *A. ollula*, *B. straminea*, *M. tuberculata* and *P. acuta*, and eight individuals of *S. quadrata*) were confined in a paper tea bag (10 x 7 cm) with twenty 3 mm diameter pores. The other three side compartments each contained an empty tea bag and served as controls. Twenty adult *P. canaliculata* (35–40 mm SL) were introduced into the central compartment. The apple snails were allowed to move towards the side compartments. The

basin was covered with a lid to prevent any directional effect of light on snail movement. After 30 minutes, the number of snails in each compartment was recorded. A comparison of the total number of snails in the control and test compartments gave a relative prey preference. The assay for each species was conducted three times.

Assays were also conducted to examine the crawling behavior of *P. canaliculata* using a rectangular (44 L x 58 W x 14 H cm) plastic tray. The tray contained a layer of clay (1 cm) collected from a semi-aquatic vegetable garden in Long Valley, the New Territories. Over the clay was 4 cm of dechlorinated tap water. The assays were conducted during the night in almost complete darkness when the apple snail was most active. Snail movement was observed with the aid of a small torch. In each assay, one adult apple snail (3.5–4.0 cm SL) was introduced into the centre of the box and its movement traced for a one-hour period, starting from the time when its muscular foot became fully extended. As the snail moved, it left a track on the clay. The track was drawn on a piece of paper and the total distance travelled measured afterwards. The 1 h assay was repeated nine times using different individuals. The water and mud were changed between assays to avoid the potential effect of snail mucus on snail movement.

Data Analysis

For each species, the effects of predator size (juvenile or adult) and prey species on consumption of egg masses, neonates or adults were assessed using two-way analysis of variance (ANOVA). The relationship between shell size and crushing weight for each prey species was established using simple linear correlation or a 2-parameter exponential growth equation, based on visual observation of the data. For each species of prey, the total number of predators (i.e., apple snails) in the controls and that in the experimental compartments were compared using a paired *t*-test, with the three assays being used as replicates.

FIG. 1. Predation of *Pomacea canaliculata* on other snails. A: Adult apple snail approaching an egg mass of *Physa acuta*. The egg mass was consumed by the predator approximately 1 minute after; B: Neonate *Melanoides tuberculata* showing a piece of flesh in the missing posterior shell; C: Neonate *Sinotaia quadrata*, showing the empty shell without an apex; D: Empty intact shell of an adult *Austropeplea ollula*; E: Empty intact shell of an adult *Physa acuta*; F: Adult *Biomphalaria straminea*, showing the broken shell and some unconsumed soft body. Scale bars A = 1 cm; B, C = 1.5 mm; D–F = 5 mm.

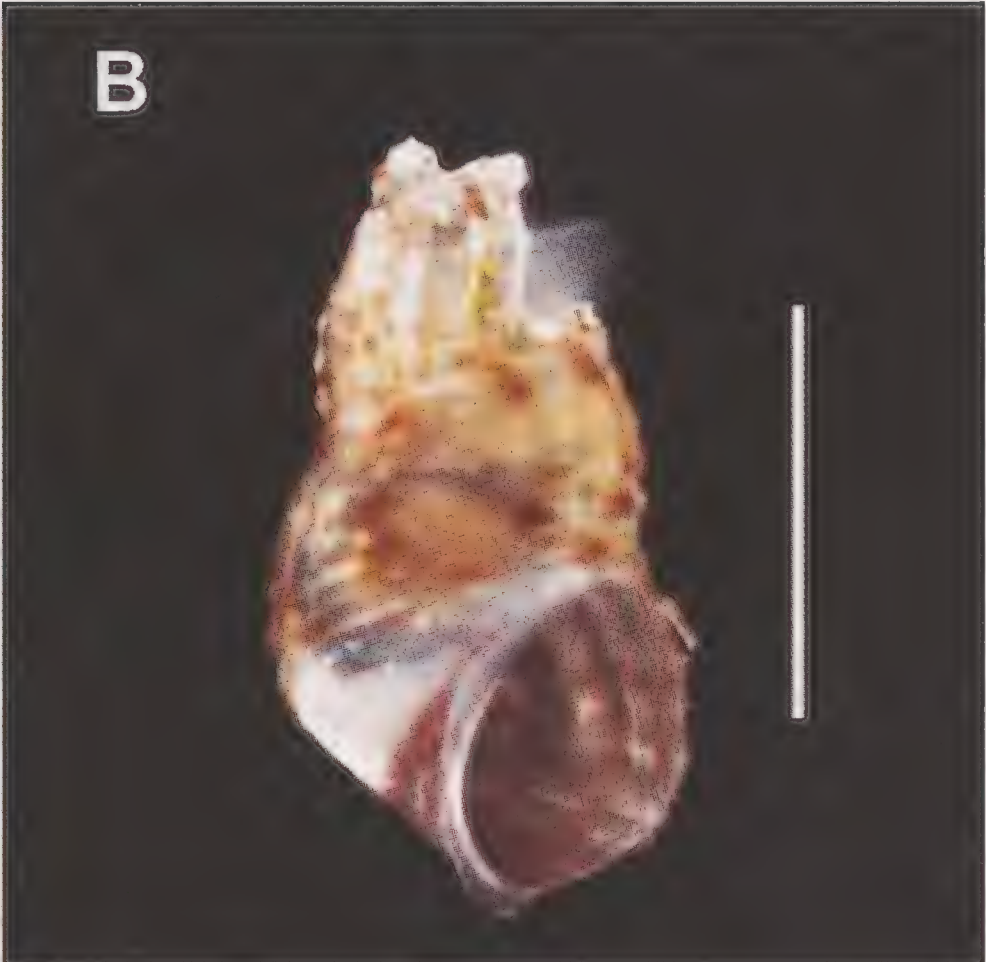
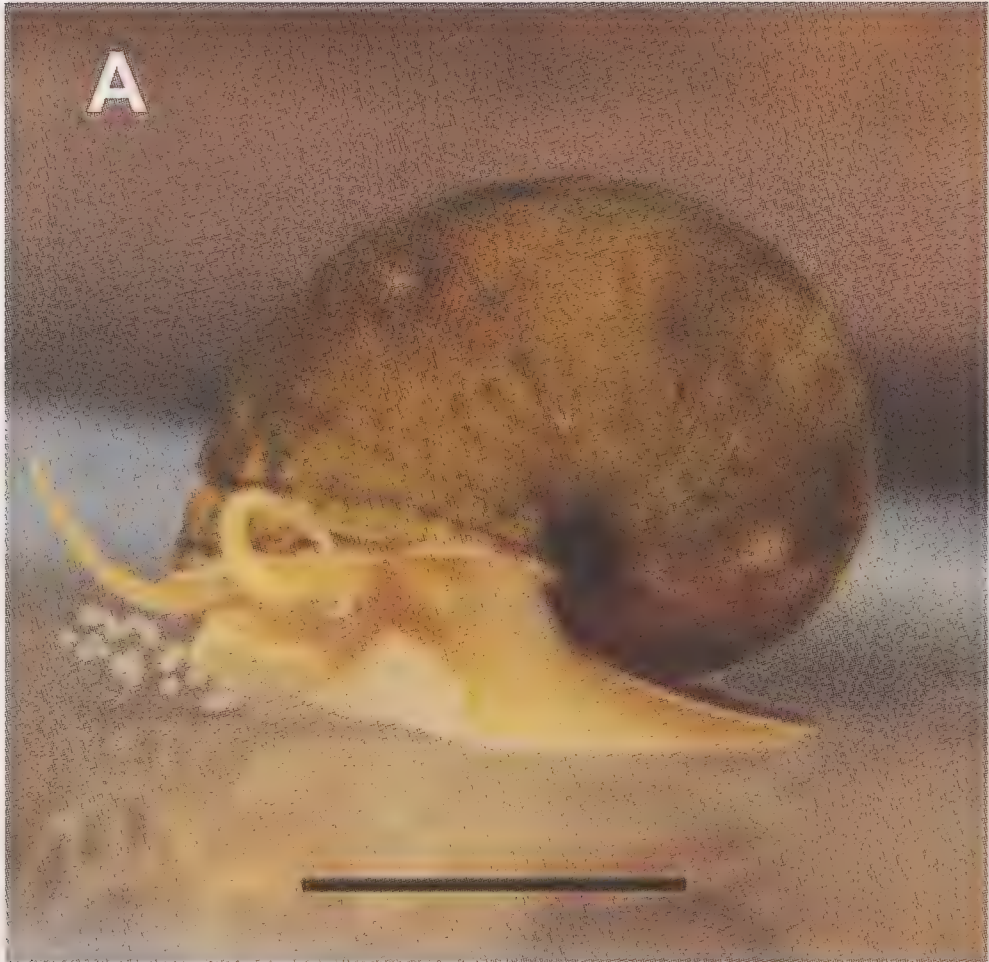


TABLE 1. Predation of *Pomacea canaliculata* on different species of prey snails. Two size classes of the predator were used. Separate tests were conducted with egg masses, neonates and adults of the preys. Two-way ANOVA was used to test effects of prey species and predator size (adult vs. juvenile) on percentage of predation. NS: not significant.

Life stage of prey	df	F	P
Experiment 1A: Egg masses			
Prey species (A)	2	32.62	< 0.0001
Predator size (B)	1	2.089	0.1665 (NS)
A x B	2	0.2206	0.8053 (NS)
Experiment 1B: Neonates			
Prey species (A)	4	24.47	< 0.0001
Predator size (B)	1	78.98	< 0.0001
A x B	4	15.30	< 0.0001
Experiment 1C: Adults			
Prey species (A)	4	4.122	0.0135
Predator size (B)	1	23.67	< 0.0001
A x B	4	4.122	0.0135

RESULTS

Experiment 1. Predation of *P. canaliculata* on Eggs, Juveniles and Adults of Potential Prey

Apple snails were observed to approach and engulf prey egg masses (Fig. 1A). Although on a few occasions part of the gelatinous matrix coating the eggs remained, the embryos were always removed. In control aquaria, all egg masses remained intact during the course of the experiment. Adult and juvenile *P. canaliculata* consumed 69–85% and 42–52% of the egg masses, respectively (Fig. 2A). The predators significantly reduced the number of egg masses, and the consumption rate of adults was significantly higher than that of juveniles (Table 1). The egg masses of the three prey species did not differ significantly in their susceptibility to predation.

In the controls, all neonate prey survived through the experiment. In the experimental treatments, adult and juvenile *P. canaliculata* consumed 22–76% and 8–48% of the neonates of the prey, respectively (Fig. 2B, Table 1). The pulmonates (31–76%) in general suffered a higher predation rate than the prosobranchs (8–42%). Adult apple snails had a significantly higher consumption rate than juveniles (Table 1). The neonates of the pulmonates (*A. ollula*, *B. straminea* and *P. acuta*) were usually entirely

engulfed, without leaving hollow shells or shell fragments. In contrast, shells of the prosobranch neonates were broken, with either some tissues remaining, as in *M. tuberculata* (Fig. 1B), or completely missing, as in *S. quadrata* (Fig. 1C).

All adult prey in the controls survived through the experiment. In the treatments, juvenile *P. canaliculata* did not consume any adult prey (Fig. 2C). The adult apple snails, however, consumed the adult pulmonates, but the consumption rate was low (33% of *A. ollula*, 24% of *P. acuta* and 27% of *B. straminea*) and not significantly different among prey species. All adult prosobranchs survived through the experiment. Examination of the dead pulmonates revealed different attack patterns. In *A. ollula* and *P. acuta*, the soft body was usually missing, but the shell was intact (Fig. 1D, E). In *B. straminea*, the shell opening and occasionally the outermost whorl were broken, with parts of the soft body, especially the head and foot, missing; the visceral mass usually remained (Fig. 1F).

Experiment 2. Size-dependent Predation of *P. canaliculata* on Two Prosobranchs

In the controls, all individuals of the two prosobranch species survived through the experiment. In the experimental treatments 14.3% of the *S. quadrata* and 12.6% of the *M.*

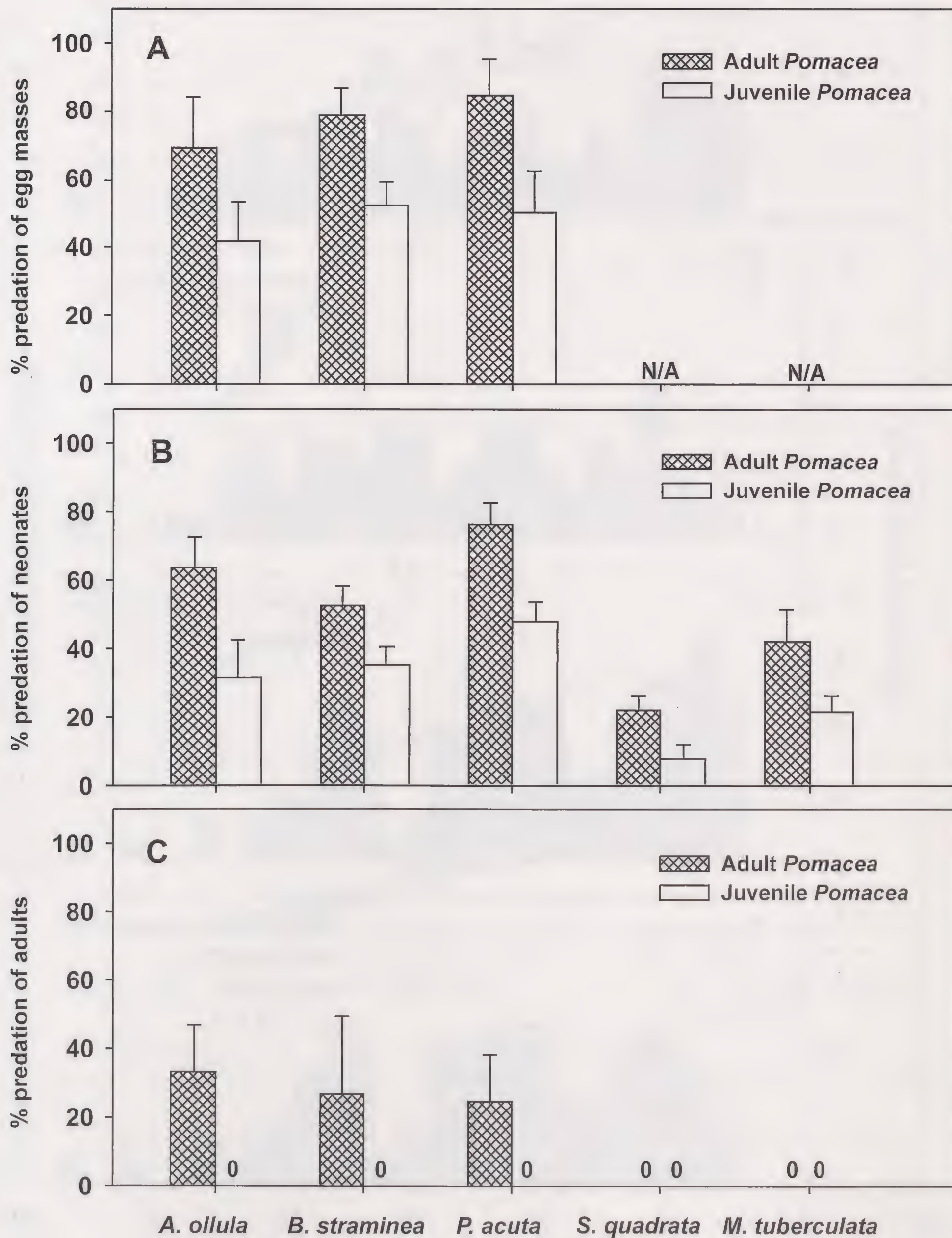


FIG. 2. Predation rate of adult (shaded bars) and juvenile (open bars) *Pomacea canaliculata* on other snails. A: Egg masses of three species of pulmonates. Data are not available (N/A) for the two species of prosobranchs, which do not lay eggs; B: neonates of five species of preys; C: adults of five species of preys. A zero represents no predatory mortality in the treatment. Each bar represents the mean of 3 replicate aquaria $\pm$ S.D.

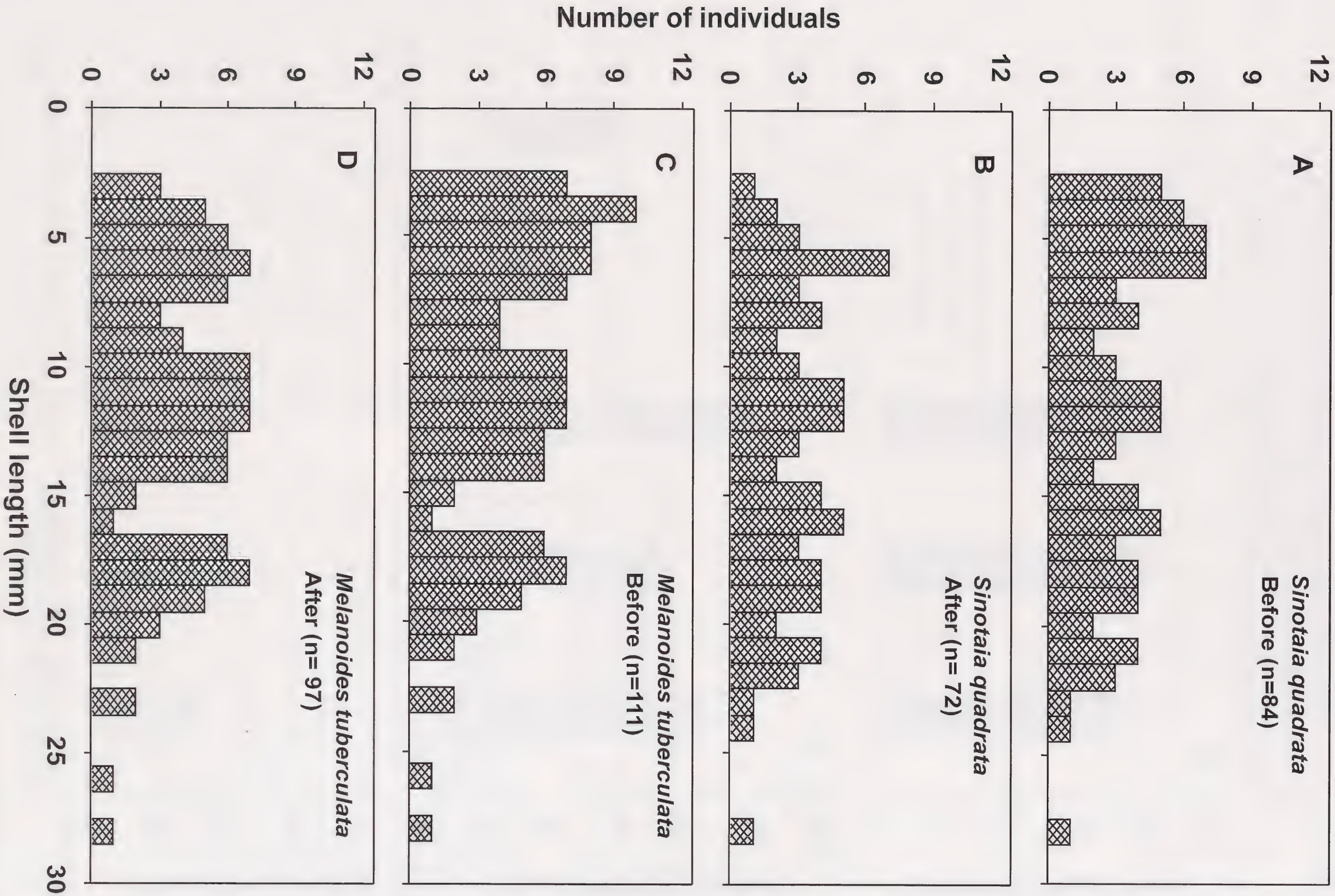


FIG. 3. Size-dependent predation of adult *Pomacea canaliculata* on the two prosobranchs. A, B: Represents the number of surviving *Sinotaia quadrata* before and after 72-h contact with the predator, respectively; C, D: Represents the number of surviving *Melanoides tuberculata* before and 72-h after contact with the predator, respectively.

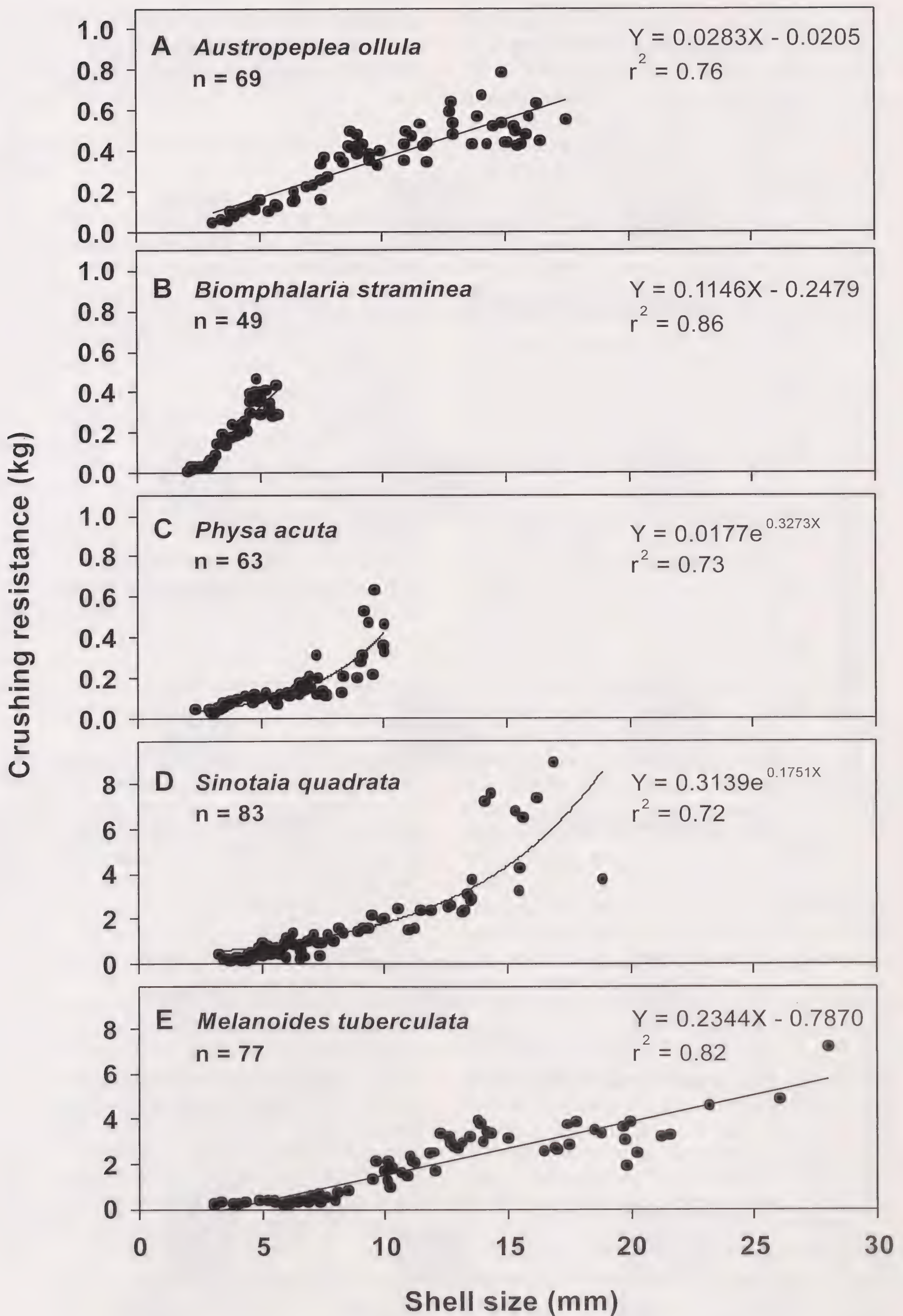


FIG. 4. Size-dependent crushing resistance in the five species of preys. The shell size refers to shell length, except for *Biomphalaria straminea*, which is shell width. The maximum adult sizes are very different among the species. Note that the scale of Y axis for the pulmonates is different from that for the prosobranchs.

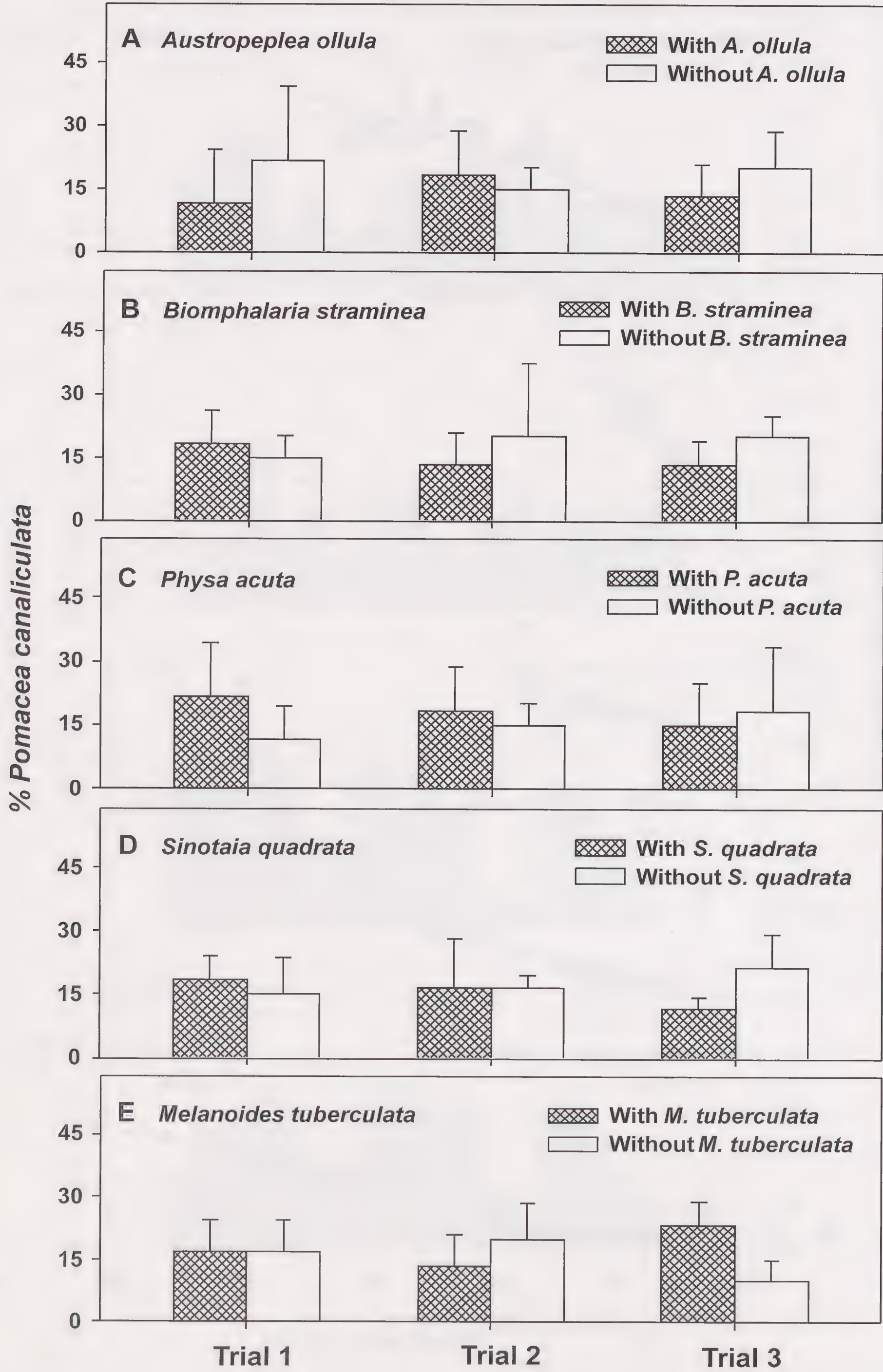


FIG. 5. Percentage of the predator in compartments containing the prey snail and those not containing the prey snail. Each species was tested in three separate assays. Each bar represents the mean of three replicate compartments $\pm$ S.D.

tuberculata were consumed, but the consumption was confined to ≤ 5 mm SL *S. quadrata* and ≤ 7 mm SL *M. tuberculata*; larger individuals were unaffected (Fig. 3).

Experiment 3. Crushing Resistance of Prey Species

For each species, the crushing resistance increased with increasing size (Fig. 4). In *A. ollula*, *B. straminea* and *M. tuberculata*, the relationship between shell size and crushing resistance could be described by a simple linear relationship. In *P. acuta* and *S. quadrata*, the relationship was exponential. The maximum crushing resistance in the three pulmonates was < 1 kg, which was equivalent to the crushing resistance of a much smaller prosobranch (6.6 mm SL *S. quadrata* or 7.6 mm SL *M. tuberculata*). The maximum crushing resistance of *S. quadrata* and *M. tuberculata* was 7.2 kg and 8.9 kg, respectively. The minimum shell length above which potential prey were safe from predation, from Experiment 2, corresponded to a crushing resistance of 0.75 kg for *S. quadrata* and 0.85 kg for *M. tuberculata*.

Experiment 4. Prey Detection and Crawling in *P. canaliculata*

The percentage of *P. canaliculata* located in the test and control compartments at the end of the experiment ranged from 10 to 23% (Fig. 5). For the five prey species, *t*-tests did not detect significant differences in the percentage of apple snails in the test and control compartments (*A. ollula*: $t = -1.11$, $P = 0.38$; *B. straminea*: $t = -1.00$, $P = 0.42$; *M. tuberculata*: $t = 0.38$, $P = 0.74$; *P. acuta*: $t = 0.87$, $P = 0.48$; *S. quadrata*: $t = -0.56$, $P = 0.64$).

In the crawling assays, the snail extended its foot fully and crawled away from the centre of the tray. Upon reaching the edge, it sometimes crawled up the wall briefly and returned to the bottom. Most of the time, it crawled on the bottom near the walls, with occasional movements toward the center. During the 1-h assay, the snail might make one or four stops. The longest stop was four minutes. Including these stops, average speed was 17.8 ± 1.7 cm min⁻¹ ($n = 9$).

DISCUSSION

Using pre-starved *Pomacea canaliculata*, Cha (1989) reported predation on the egg masses and neonates of *B. straminea*, as

well as the neonates of *A. ollula*, *P. acuta*, and *M. tuberculata*, but not on the neonates of *S. quadrata*. In our study, non-starved *P. canaliculata* fed on the neonates of all these species, although the consumption rate on *S. quadrata* was much lower than that on other species; they also consumed the adults of the three pulmonates. These results indicate that *Pomacea canaliculata* is a generalist predator of freshwater snails belonging to different families. Several other ampullariids are known to prey on various life stages of other snails. For example, *Pomacea bridgesii* ingested the eggs of *Indoplanorbis exustus* (Planorbidae) (Aditya & Raut, 2002), *Lanistes varicus* consumed the eggs and neonates of *Biomphalaria pfeifferi* (Planorbidae) (Anto et al., 2005), and *Marisa cornuarietis* preyed on the eggs, juveniles and adults of *Bulinus truncatus* (Planorbidae) (Demian & Lutfy, 1965a), juveniles and adults of *Lymnaea caillaudi* (Lymnaeidae) (Demian & Lutfy, 1966), eggs and neonates of *Biomphalaria glabrata* (Cedeño-León & Thomas, 1983), and eggs and neonates of *Biomphalaria alexandrina*, but not its adults (Demian & Lutfy, 1965b). Most of these prey species studied, however, belong to the Lymnaeidae and Planorbidae, which are intermediate hosts of human parasites, especially *Schistosoma*. The only practical way of combating these parasitic diseases is to control their vector snails (Dillon, 2000). Biological control using predators is traditionally conceived as environmentally friendly because it does not require the use of toxic chemicals, it is usually cheaper and its effects are long-lasting (Cowie, 2001). In fact, a number of field studies have demonstrated the usefulness of some ampullariids in controlling the populations of these vectors (reviews by Dillon, 2000; Cowie, 2001).

Due to the emphasis on human health, these previous studies have focused on the efficacy of predation, that is, whether the vector snails can be removed. Consequently, little information is available on the impact of these ampullariids on non-target snails (Cowie, 2002). Although anecdotal observations have linked the invasion of *P. canaliculata* to the decline of *Pila* spp. (Ampullariidae) in southeast Asia (Acosta & Pullin, 1991; Halwart, 1994), Cha (1989), our study is the first to provide experimental evidence of its relatively non-selective predation on several life-stages of various freshwater gastropod species, some of which are important detritivores in freshwater wetlands (Dudgeon & Yipp, 1985). The predation rates varied with the life stage of the predator,

and the species and life stage of the prey. But in general, these rates were high, with daily consumption of an adult apple snail ranging from 21.0 (*A. ollula*) to 26.2 (*P. acuta*) egg masses, 1.5 (*S. quadrata*) to 5.2 (*P. acuta*) neonates, and 0.0 (*M. tuberculata* and *S. quadrata*) to 0.6 (*A. ollula*) adults. Cazzaniga (1990) reported an adult *P. canaliculata* killing only 0.067 ± 0.014 adult *Biomphalaria peregrina* per day, perhaps due to the large shell of the prey (9–13 mm). An adult *Pomacea bridgesii* consumed only around three egg masses of *Indoplanorbis exustus* per day, probably due to the lower predatory potential or smaller size of *P. bridgesii* compared to *P. canaliculata* (Aditya & Raut, 2002). High consumption rates have been reported in studies of other ampullariids. For example, Anto et al. (2005) reported that an adult *Lanistes varicus* ate up to 200 eggs masses and 1.8 neonates of *Biomphalaria pfeifferi* per day. Cedeño-León & Thomas (1983) reported that an adult *Marisa cornuarietis* devoured up to 50 egg masses of *Biomphalaria glabrata* per day.

Availability of macrophytic food may affect predation by ampullariids, but evidence as to whether it will enhance or reduce predation is inconsistent. For instance, Cedeño-León & Thomas (1983) reported that juvenile (17–23 mm) *Marisa cornuarietis* did not consume *Biomphalaria glabrata* eggs in the absence of macrophytic food. But once the macrophyte supply was resumed, it fed with a rate of 1.9 egg masses per snail per day. This primarily macrophytophagous snail may therefore need a minimum amount of macrophytic food to maintain its vigour for intensive browsing and/or predation. Nevertheless, Demian & Lutfy (1966) showed that an adult *Marisa cornuarietis* consumed only 0.29 adult *Bulinus truncatus* per day when fed with excess lettuce, but the consumption rate rose to 0.68 individuals per day in the absence of lettuce. Whether the relatively high predation rates in our experiments are due to the presence of lettuce is unknown, but they are lower than those reported by Cha (1989), who conducted the experiments with pre-starved *P. canaliculata* adults and found consumption rates of up to 180 egg masses and 31 neonates of *B. straminea* per day per individual.

To understand the impact of an invasive species on an invaded ecosystem, it is essential to collect empirical evidence of its interaction with indigenous species. But from a predictive perspective, it is perhaps more important to know how the invasive species affects indigenous species. *Pomacea canaliculata* can detect the presence of macrophytic food (i.e., *Elodea canadensis*, *Myriophyllum elatinoides*,

Rorippa nasturtium aquaticum and *Zannichellia palustris*) from a distance of 30 cm (Estebenet, 1995). Romaine lettuce can also effectively attract *P. canaliculata* from a distance of 20 cm (Kwong, personal observation). Nevertheless, this study did not indicate that *P. canaliculata* could detect its prey from a distance. It appeared to crawl randomly in the aquaria. But direct contact of its tentacles with the prey did occasionally trigger an attack. The question thus remained as to whether such random crawling would create sufficient encounters between the predator and the prey. Dudgeon & Lam (1985) studied the crawling of seven species of freshwater gastropods in Hong Kong, four of which were used in this study. The mean crawling speed of *Biomphalaria straminea*, *Melanoides tuberculata*, *Physa acuta*, and *Sinotaia quadrata* was 3.73, 2.09, 6.76 and 2.25 cm min⁻¹, respectively. These rates of movement were far below that of *P. canaliculata* (17.8 cm min⁻¹). Based on a conservative 8-h active period per day, assuming the snail is only active at night, an adult foot width of approximately 2.5 cm, and a crawling speed of 17.8 cm min⁻¹, we estimate that the crawling of an adult *P. canaliculata* would cover an area of 2.1 m². Therefore, although this species cannot detect, or at least is not attracted to the water-borne cues released from other freshwater snails, it may still pose a threat to other snails due to its rapid crawling behavior.

The five prey species tested in this study differed greatly in their vulnerability to predation by *P. canaliculata*. The pulmonates appeared more vulnerable than the prosobranchs. Such differential vulnerability may be explained by the effectiveness of their defence. In general, a snail responds to a threat of predation in one of three ways: withdrawal of its head-foot into the shell, clinging tightly onto the substratum, or shaking its shell (reviewed by Dillon, 2000). The adaptive nature of the first two responses is obvious, but that of the latter may be best explained by the work of Townsend & McCarthy (1980), who studied the responses of *Physa fontinalis* upon direct contact with the tissue of molluscivorous leeches. The prey snail shakes its shell vigorously, followed by detachment of its foot from the substratum. Depending on whether this shaking results in enclosing an air bubble from the environment or spilling an air bubble held by the snail, the snail can float to the surface or sink to the bottom, thus escaping predation.

These three types of responses were all observed in this study. The two species of prosobranchs responded to contact with

Pomacea canaliculata by simply withdrawing their head-foot, pulling their operculum behind to close the shell. Sometimes *P. canaliculata* was seen to wrap the prey with its foot, and appeared to move its mouth and radula on the shell. Apparently due to the large size, hard shell and an operculum in these prey, the attacks always failed. After a brief encounter, the predator would move away. The three pulmonates responded differently. *Biomphalaria straminea* reacted initially by clinging onto the substratum. The predator might simply move the foot and body over the prey, leaving the *B. straminea* unharmed. Sometimes the predator twisted its foot, thus dislodging the prey from the substratum. The prey then retracted its head-foot. Occasionally the predator would initiate an attack by attempting to introduce its head into the shell aperture. Probably due to the small size of the prey and its fragile shell, the defence behaviours of *B. straminea* appeared ineffective. The shell aperture was usually broken. Due to the small aperture of the shell, some tissue usually remained uneaten. Other types of shell damage, as reported for *B. peregrina* (Cazzaniga, 1990), were only occasionally seen. Adult *Physa acuta* responded by shell-shaking. *Austropeplea ollula* held firmly onto the substratum and lowered its shell to minimize exposure. Both species have a large aperture but lack an operculum and thus are vulnerable when turned upside down. However, these two pulmonates tend to float on the air-water surface, which could reduce the chance of encounter with the predator. Sometimes an attack would be initiated if the predator was able to move its foot on top of the prey. The attack was similar to that on *Bulinus truncatus* by *M. cornuarietis* (Demian & Lutfy, 1965a). The predator would use its foot to orient the shell of the prey such that it could push its head into the shell aperture and use its radula and jaws to snip off the soft body of the prey. The predator would sometimes pull out the whole soft body. This attack behaviour therefore usually left an intact but empty shell.

Our experiments were conducted in the laboratory so no refuges were available. In the natural environment, plants, stones, and sediment might reduce the efficiency of predation. Also, in temperate and subtropical areas, *P. canaliculata* suffers high mortality and appears to aestivate during the winter (Cowie, 2002; Estebenet & Martín, 2002), which might allow the juveniles of some winter-breeding species to reach a size refuge and thus escape predation by *P. canaliculata*. In fact, *Sinotaia quad-rata* is often found to co-exist with apple snails

in lowland water bodies in the New Territories, Hong Kong. It carries fully developed hatchlings throughout the year, and birth mostly occurs in the warmer months (Dudgeon & Corlett, 2004), although we have seen small numbers of neonates in the winter (Kwong, unpublished data). Nevertheless, given its high crawling speed and relatively non-discriminating attacking behaviour, the possible predatory effect of *P. canaliculata* on freshwater snails, especially those with a fragile shell, should not be overlooked. In a 2 m cage study in an outdoor pond, introducing *P. canaliculata* caused a remarkable reduction in the density of six out of eight species of freshwater snails (Wong et al., in press). Taken together, the results of these field and laboratory studies indicate that predation by *P. canaliculata* may have a high potential for reducing the diversity of freshwater snails. This study provides further evidence supporting the precautionary principle when considering this and other ampullariids as biological control agents of snail vector of human parasites or aquatic weeds (Cowie, 2001).

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